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Abstract

For moving animals, the successful avoidance of hazardous obstacles is an important capability. Despite this, few models of collective motion have addressed the relationship between behavioural and social features and obstacle avoidance. We develop an asynchronous individual-based model for social movement which allows social structure within groups to be included. We assess the dynamics of group navigation and resulting collision risk in the context of information transfer through the system. In agreement with previous work, we find that group size has a non-linear effect on collision risk. We implement examples of possible network structures to explore the impact social preferences have on collision risk. We show that any social heterogeneity induces greater obstacle avoidance with further improvements corresponding to groups containing fewer influential individuals. The model provides a platform for both further theoretical investigation and practical application. In particular, we argue that the role of social structures within bird flocks may have an important role to play in assessing the risk of collisions with wind turbines but that new methods of data analysis are needed to identify these social structures.

1 Introduction

Collective motion can be observed in a wide variety of biological systems, inspiring scientists to investigate the mechanics behind such apparently complex behaviour [1–4]. Many of these studies have developed individual-based models to assess the effect of behavioural and environmental factors [5–9]. These models simulate motion through local interactions by applying rules based on proximity with individuals exhibiting three core behaviours: repulsion (avoiding collision with other individuals); orientation (aligning with nearby individuals); and attraction (movement towards distant individuals) [5, 10]. Additional rules can be incorporated to represent environmental factors, for example, navigation towards a target or response to predators [6–8, 11].

Typically, such individual-based models do not constrain the number of interactions that contribute to the motion of an individual. These are known as “metric” models, as they sum the interactions with all cues within a given distance of a focal individual [6, 7, 9]. However, empirical evidence suggests that social interactions may in fact be topological, with each individual responding only to a fixed number of other individuals [12]. Studies which develop an asynchronous updating method have demonstrated that this topological property for interactions emerges spontaneously [8]. Signif-

21 icant features of this modelling approach include varied speed distributions
22 and emergent stochastic noise in the decision making process, both of which
23 contribute to a greater degree of biological realism.

24 The importance of this updating scheme becomes apparent when indi-
25 viduals interact with other environmental factors and averaging becomes
26 inappropriate. Of particular interest is when these environmental factors are
27 of significant societal or conservational relevance. For example, a growing
28 demand for renewable energy has led to a significant increase in the num-
29 ber of wind farm developments [13]. Wind farms are often sited in areas
30 which intersect existing flight paths of migratory bird species, thereby form-
31 ing a potential barrier to movement [14]. It is important that we understand
32 the impact such developments could have on the level of avian mortality
33 as a direct result of collisions in order to protect the population of at risk
34 species [15]. There is considerable variability in the collision risk for avian
35 species from wind turbines, not least due to variable sampling techniques
36 and carcass loss from scavengers, estimates for per turbine collision rates per
37 annum span 4 orders of magnitude [15]. However, few studies in the field
38 of collective motion have investigated the interactions of bird flocks with
39 wind turbines or other obstacles [16, 17], primarily because of ambiguity in
40 the methodology for incorporating obstacles (and their avoidance) within
41 existing models.

42 Previous work investigating the interaction of groups with a single ob-
43 stacle shows that group size has a non-linear relationship with collision risk,
44 and that whilst initially social interactions cause a higher per capita risk of
45 collision this is reduced with further increases [9]. This has implications for
46 the modelling of real-world applications, especially for avian collisions where
47 current probabilistic models [18] have no explicit dependence on group size
48 and cannot incorporate changes in behaviour driven by social dynamics [19].

49 Recent studies using an asynchronous update scheme have outlined a
50 robust framework to investigate the effect of complex behaviours such as
51 the influence of social networks [20]. This has important applications in
52 simulating real-world animal movement where empirical evidence suggests
53 that both ability and influence are unlikely to be distributed evenly [21–23].
54 The results show that when compared to previous studies, which focus on
55 the effects of varied ability [6, 24, 25], underlying networks representing sim-
56 ple examples of leadership can have a significant impact on group dynamics
57 and navigational performance. Whilst leadership provides one example of
58 a social network structure, other characteristics such as clustering, as a re-
59 sult of strong interactions between members of family groups, could also be
60 present and have the potential to produce distinct group behaviours. This

61 highlights the importance of identifying plausible network structures in or-
62 der to produce realistic simulations of animal movements. In the case of
63 geese such networks structures are not well established; and in pigeons it
64 has been shown that in-flight hierarchies cannot be inferred reliably from
65 ground-based networks [23]. Network structures in other systems are better
66 developed, for example in humans [26], in other social animals [27] and in
67 other application areas [28, 29].

68 Here, we describe an individual-based model with an asynchronous up-
69 dating algorithm to investigate group interactions with obstacles. Using this
70 model we explore the response of individuals to changes in group size. We
71 determine the effect this may have on collision risk; initially with a single
72 obstacles, and then with an array of obstacles representing a typical wind
73 farm. We parametrise and then continue to simulate group interactions with
74 an obstacle array, investigating the impact underlying social networks have
75 on collision risk by comparing four example networks (homogeneous, ran-
76 dom, clustered and leadership; to be defined in Methods) each representing
77 a distinct structural characteristic. We discuss how different environmental
78 factors may contribute to collision risk paying particular attention to the role
79 of weather conditions, such as environmental turbulence and visibility. These
80 factors have proved difficult to assess empirically as many studies rely upon
81 a degree of visual observation to determine behaviour [15, 30, 31]. Finally,
82 we investigate the trade-off between avoidance and migratory pressures such
83 as energetic efficiency [32] by introducing a fixed straight route which group
84 members attempt to follow, thereby minimising energy expenditure. Such
85 behaviour imposes a previously ignored cost to obstacle avoidance which may
86 have an important impact on predicted collision risk.

87 **Methods**

88 **Modelling Framework**

89 The model is adapted from the stochastic implementation outlined in [20].
90 Groups consist of a set of $\{1, \dots, N\}$ individuals each represented by a posi-
91 tion \underline{x}_i and a unitary heading vector $\hat{\underline{v}}_i$ in continuous two dimensional space.
92 Inspired by computational techniques for object reconstruction, obstacles are
93 represented by a finite set of $\{1, \dots, M\}$ vertexes and connecting edges [33].
94 Each obstacle vertex is represented by a position \underline{p}_i and an outwardly facing
95 normal vector $\hat{\underline{n}}_i$. By describing obstacles in this way we provide a flexible
96 approach for approximating any shape, size or orientation without the need
97 for complex differential geometry. The degree of error in this method can be

controlled by varying the number of vertices which comprise each obstacle. This allows us to distinguish between obstacles of equal size which induce different avoidance potentials, for example as a result of varying levels of transparency. In this study we minimise the error in behavioural response by adopting a standard spacing of 1 spatial unit between vertices; provided the minimum distance used to categorise behavioural response is greater than this value individuals will detect the obstacles and react appropriately. Motivated by our wind turbine application, obstacles are considered to be transparent to the extent that they do not occlude vision.

In common with established models [5, 6, 10] an individual determines a direction of motion by responding to selected navigational cues within a given sensory zone, including migration towards a particular target. This sensory zone is defined by a circle of radius R_a centred on the individual, with an omitted blind angle β to the rear [34]. However, unlike these models, individuals are updated asynchronously according to the following algorithm:

1. Choose individual i at random.
2. Choose an “update partner” j (which may be another individual, an obstacle vertex, or the target direction) with probability P_{ij} at random from all stimuli within sensory zone (see below). If there is no stimulus then continue on current heading.
3. Determine \hat{v}_i in response to chosen partner j .
4. Update \underline{x}_i and \hat{v}_i .

We ensure that each individual updates on average once per time interval Δt by performing N realisations of the steps 1-4 [35]. Simulation outputs are recorded every $\tau = \lambda \Delta t$ seconds, where $\lambda (\geq 1)$ defines the average number of updates performed by each individual. When $\lambda > 1$ the resulting behaviour between consecutive model outputs is the sum over a number of updates [20]. The choice of λ is discussed in table 1.

The probability of an individual selecting a particular update partner is initially weighted based on the type of interaction. Interaction weighting are defined as social (w_s), obstacle (w_o) and target (w_t). Each of these weightings is modified according to a spatial relationship providing distinction between partners of the same type. Social and obstacle interactions are each scaled by a factor equal to the inverse of relative distance ($d_{ij} = |\underline{x}_j - \underline{x}_i|$); capturing the averaged effect of visual occlusion. In addition, obstacle vertices which appear outside of the frontal region defined by a sector of angle α and radius greater than R_r^o are considered to have a weighting of zero.

135 In order to emulate the effect of social networks within the group we
 136 construct an underlying fixed matrix with elements e_{ij} (≥ 0). This matrix
 137 remains unchanged through the simulation and contains information on the
 138 long-term social preference and bonds between group members. The factor
 139 $\epsilon_{i,j}$ further scales the probability of an individual i selecting a particular
 140 neighbour j . The details and implications of this methodology are discussed
 141 in detail elsewhere [36,37].

142 Finally, the weighting for target navigation comprises two parts, a con-
 143 stant directional part (w_{t0}), and a variable part (w_{t1}) which is determined by
 144 a function of the angle between the individuals current heading and its ideal
 145 target direction (ϕ). As an individual orientates away from its ideal target
 146 heading this angle becomes greater, increasing the target selection weighting.
 147 This simulates a desire for group members to follow a particular route with
 148 strong route fidelity, a well established trait of migratory birds (e.g. [38]).
 149 In summary, for an individual i in a group with individuals $n = \{1, \dots, N\}$
 150 augmented with the obstacle vertices $m = \{1, \dots, M\}$ and the target, then
 151 update partner $j \in \{1 + N + M\}$ is chosen with probability:

$$P_{ij}^s = (\frac{w_s e_{ij}}{d_{ij}})w^{-1}, \quad P_{ij}^o = (\frac{w_o}{d_{ij}})w^{-1}, \quad P_{ij}^t = (w_{t0} + w_{t1}(1 - \cos(\phi))w^{-1}$$

152 where w is the sum of weighting for all stimulus. P_{ij}^s , P_{ij}^o , P_{ij}^t denote the
 153 probabilities for social, obstacle and target interactions respectively. It is
 154 important to note that this differs from previous implementations of this
 155 model [20] which use a constant probability for the target; here the target is
 156 merged into the pool of update partners that can occur at each micro-step,
 157 and as a result the target preference is dependent upon the weight of other
 158 stimuli.

159 Once a partner has been selected, the updating individual must deter-
 160 mine how to respond according to the type of update partner. If a neighbour
 161 is selected, then the focal individual's sensory zone is divided into hierar-
 162 chical interaction zones of radius R_r^s , R_o^s and R_a which dictate whether
 163 repulsion, orientation or attraction manoeuvres are performed respectively.
 164 Here, attraction manoeuvres are applied with a velocity of $2v_0$, represent-
 165 ing the increased thrust required by an individual to reduce their distance
 166 to neighbours, maintaining group cohesion. Similarly, if an obstacle vertex
 167 is selected a repulsive manoeuvre is applied within a zone of radius R_r^o .
 168 For any vertices which appear at a distance greater than R_r^o we apply a
 169 pre-emptive avoidance strategy equivalent to social alignment which aims
 170 to limit more extreme repulsive action. Previously, it has been proposed

171 that individuals should attempt to align themselves with the surface of an
172 obstacle at the point of interaction [9]. For birds, which have been shown
173 to have largely monocular vision [17], this type of information requires a de-
174 gree of depth perception that is likely to be beyond their sensory capability.
175 Instead, in this model we suggest a simpler response where individuals turn
176 away from obstacle vertices to maintain a minimum angle of α between their
177 heading and the trajectory intersecting the vertex. The cumulative effect of
178 this response results in an individual attempting to avoid an obstacle on a
179 trajectory which requires the least deviation from its current heading.

180 If target navigation is selected then an individual aims for a point that
181 is a fixed distance (d_t) from its current projected position along the group
182 target trajectory, inspired by route fidelity found in other species. This
183 target trajectory is defined by the straight line starting at the initial group
184 centre of mass and continuing indefinitely in the direction specified by a fixed
185 target vector (\hat{v}_t). This implements instantaneously perfect navigation on a
186 linear route. Other studies have considered error in navigation [7], but when
187 this variation is introduced into the model presented here it is dominated
188 by the inherent noise in the underlying algorithm [39]. For the application
189 to collision avoidance, navigation error is therefore of less importance than
190 some of the other features varied in our analysis.

191 To represent the finite ability of an individual to execute a turn in the
192 direction of its preferred heading, we implement a maximum turning rate of
193 θ . In simulations which apply a movement error to represent environmental
194 turbulence we rotate the calculated heading vector, following the application
195 of a turning limit, by an angle randomly drawn from a Von Mises distribution
196 with mean of zero and equivalent standard deviation w_e . Intersections with
197 obstacles are recorded when the trajectory of an individual intersects either
198 an obstacle vertex or connecting edge. In this implementation of the model
199 we consider the probability of these intersections resulting in a fatal collision
200 to be zero. Consequently, intersecting individuals are not removed from
201 simulations.

202 We compute various metrics to summarise the data from our simulations.
203 **Target navigation ability** is defined as the fraction of the trajectory that
204 all birds spend travelling to the target direction. This is computed as the
205 dot product of the mean group direction with the target direction, scaled by
206 the mean distance traveled, averaged over the simulation. The **probability**
207 **of splitting** is computed by calculating the fraction of simulations which
208 contain more than one group at a fixed time period after passing the line
209 $y = 0$. This include both spontaneous splitting and interaction with the
210 obstacle to enable a measure of relative disruption to be computed. The

number of groups is calculated using an equivalence class relation with the equivalence based on the radius of alignment. The **probability of avoidance** is computed by averaging the number of individuals which intersect a single wind turbine (micro) or array of wind turbines (macro) across all independent simulations of a given scenario. The latter measure is utilised in all except figure 2(a), as noted in the captions.

Parameterisation

Parameters are chosen to nominally represent flocks of pink-footed geese (*Anser brachyrhynchus*) interacting with an array of wind turbines. Where possible parameter values have been taken from empirical data. Time and space steps, and model parameters, are related to their real world units and values in Table 1. Following [40] the width of obstacles used in simulations is fixed at 100 metres, which represents a typical offshore wind turbine.

In simulations where we investigate the effect of heterogeneity in the abilities of group members, the values of obstacle avoidance and target preference are varied. For each individual the parameters stated in table 1 are scaled by a value randomly selected from a normal distribution with mean equal to 1 and standard deviation w_h , which provides a quantification for heterogeneity.

In order to simulate underlying social networks we define interaction matrices with elements e_{ij} denoting the strength of the social connection individual i has towards neighbour j . For a **unitary homogeneous network** we consider connections between neighbours to have a weight equal to 1 ($e_{ij} = 1$). Connections between the same individual are disallowed ($e_{ii} = 0$). **Random networks** are generated relative to this unitary matrix so as to maintain a balance between the average weight of all detected social interactions relative to obstacle and target interactions. Initially, we assume that all individuals are at least weakly connected with weight w_n . Connections are selected at random and incremented by w_n until the sum of all elements is equal to that of the homogeneous case.

For **clustered and leadership networks** the connections which can be incremented are limited to a specific subgroup. In the case of a leadership network l individuals are randomly identified as leaders. The only matrix elements which can be incremented are those which describe the connections from a remaining group member to any of these leaders. In the case of clustered networks, group members are assigned a number between 1 and c representing a fixed number of subgroups. The only matrix elements which can be incremented are those which describe the connections between group

249 members with matching cluster index. Unless otherwise stated simulations
250 use a unitary homogeneous network.

251 Simulations

252 Simulations consist of two phases: an initial warm up, followed by a phase
253 of interaction with obstacles. Each phase is performed for a period of 1000
254 time steps in an unbounded environment. The warm up phase allows groups
255 to form a representative configuration in the absence of obstacles. Here, we
256 define a representative configuration to mean that all individuals belong to an
257 equivalence class where neighbours are declared equivalent if they are within
258 a distance equal to the radius of alignment (R_o^s). Thereby, each individual
259 must as a minimum be in a position to align with at least one neighbour.
260 It should be noted that individuals can become permanently separated from
261 the main group. In such cases where a representative configuration is not
262 formed the warm up phase is repeated.

263 The group is then reset with its centre placed on a selected origin and
264 rotated so that the average heading is equal to the specified target direction.
265 In simulations with a single obstacle we use a fixed origin which is located
266 5000 metres from the obstacle centre in the target direction. Otherwise,
267 groups interact with an array containing 25 obstacles uniformly arranged
268 on a square grid at 500 metre intervals, the representative spacing of wind
269 turbines [44].

270 To focus on behavioural effects and minimise the effect of starting condi-
271 tions we perform the following randomisation scheme on the initial positions.
272 The origin is randomly selected on a line segment with midpoint 6000 metres
273 from the array centre (approximately 5000 metres from the nearest obsta-
274 cle) in the target direction and extending perpendicular to this vector. The
275 group centre may be placed either side of the segment midpoint at a distance
276 corresponding to the cross-sectional width of the obstacle array excluding a
277 50 metre buffer zone at both ends. This guarantees that, if there is no avoid-
278 ance behaviour, individuals will intersect the area bounding the array. By
279 varying the origin of groups we sample all potential interactions with the
280 array. To minimise the number of direct routes through the array we offset
281 the angle of approach, between the target direction and the orientation of
282 columns in the array, by 12 degrees, at which the probability of an individual
283 avoiding all obstacles without evasion is negligible.

284 Once the simulation warm up phase is complete, the phase of obsta-
285 cle interaction is initiated, during which individual level trajectory data is
286 recorded at discrete time intervals (τ). For each set of parameters we per-

Symbol	Value	Description and Unit (where appropriate)
N	30	Number of individuals within the group [9].
τ	1	Time interval for each individual to perform, on average, λ updates (in seconds) [8, 20].
Δt	0.01	Time interval for each individual to perform, on average, a single update step (in seconds) [8, 20].
λ	100	Update frequency represents the average number of updates an individual performs per second [8, 20, 41].
v_0	15	Average cruise speed in metres s^{-1} [32].
α	45	Angle of pre-emptive obstacle avoidance needed to observe a minimum distance of R_r^o from vertexes.
β	60	Angle of rear blind region of an individual (in degrees) [34].
θ	80	Maximum horizontal turning rate (degrees s^{-1}) [32].
R_r^s	2	Radius of social repulsion, in metres, representing the average size of an individual, in this case the wingspan [32].
R_r^o	150	Radius of obstacle repulsion, in metres, average minimum distance maintained by individuals from obstacles, in this case geese from wind turbines [30].
R_o^s	20	Radius of social alignment, in metres, maximum nearest neighbour distance within groups, in this case flocks of geese [42].
R_a	1000	Radius of attraction, in metres, representing the maximum perception distance of an individual, in this case the maximum distance from wind farms which geese show avoidance action [43].
w_s	1	Social preference weighting, the priority an individual shows towards selecting a neighbour for an “update partner”.
w_o	1	Obstacle avoidance weighting, the priority an individual shows towards selecting an obstacle vertex for an “update partner”.
w_t	0.1	Target preference weighting, the priority an individual shows towards selecting the target for an “update partner”.
w_{t0}	0.1	Baseline target preference weighting, the minimum weighting which guarantees successful navigation towards a designated target.
w_{t1}	0	Variable target preference weighting, the coefficient which scales the maximum target preference weighting.
w_n	0.1	Network weighting, the magnitude of increments applied to interaction matrix elements used in random network generation.
w_h	0	Heterogeneity, the standard deviation of the normal distribution used to vary avoidance and target preferences between individuals.
d_t	30000	Target heading distance, defines the distance along group target trajectory which an individual navigates towards. This is chosen to minimise the lateral effect on group structure.

Table 1: List of parameters used in model simulations. Values stated are for a typical group interacting with a square array of 25 obstacles. Where appropriate, physical parameters have been set based on values from existing empirical studies.

form 100 iterations and using this trajectory data calculate the statistics characterising group dynamics and collision risk.

Results

Prior to introducing any obstacles, the first step is to establish what baseline target preference is necessary for the model to reproduce the observed biological phenomenon of coherent group navigation along a nominated trajectory. Figure 1 summarises this process: Panel (a) confirms that the minimum target preference required, relative to a social weighting of unity, is approximately 10^{-2} ; Panel (b) shows that group cohesion is initially improved by a common navigational direction but that there exists a maximum baseline target preference of approximately 10^{-1} , above which relative social preference is insufficient to maintain group cohesion. Combining these results we identify this maximum threshold as an appropriate value for baseline target preference across all group sizes. In addition to the results shown in figure 1 we observe that mean nearest neighbour distance decreases as a function of group size, consistent with Hemelrijk and Hildenbrandt [45].

We can now begin to explore the effect of avoidance preference in relation to collision risk (Figure 2). In common with a simpler fixed time step model [9], we find that avoidance is dependent upon group size, with smaller groups displaying an increased ability to avoid both single obstacles and arrays across all parameter values. Furthermore, it can be seen in figure 7 that this relationship can be non-linear. In the context of avian interactions with wind turbines we aim to identify a suitable parameter value for avoidance preference by comparing the data in figure 2(b) to estimated wind farm avoidance rates for migrating geese. This plot shows a sharp improvement in avoidance around a value of 1 with an average probability of avoidance across all group sizes reaching approximately 60%. This lies well within the range of estimates for wind farm avoidance observed by empirical studies which record values between 50 and 70% [46]. Empirical studies also observe that of the remaining individuals which enter the wind farm area more than 99% successfully avoid all wind turbine structures resulting in an overall avoidance rate of approximately 99.8% [31, 47]. However, it should be noted that there are some studies which record 100% avoidance [30] – for our chosen value of $w_o = 1$ individuals entering the array are able to successfully avoid all obstacles.

Using the parameter values identified above for all subsequent simulations we explore the effect that heterogeneity within a group has on collision risk.

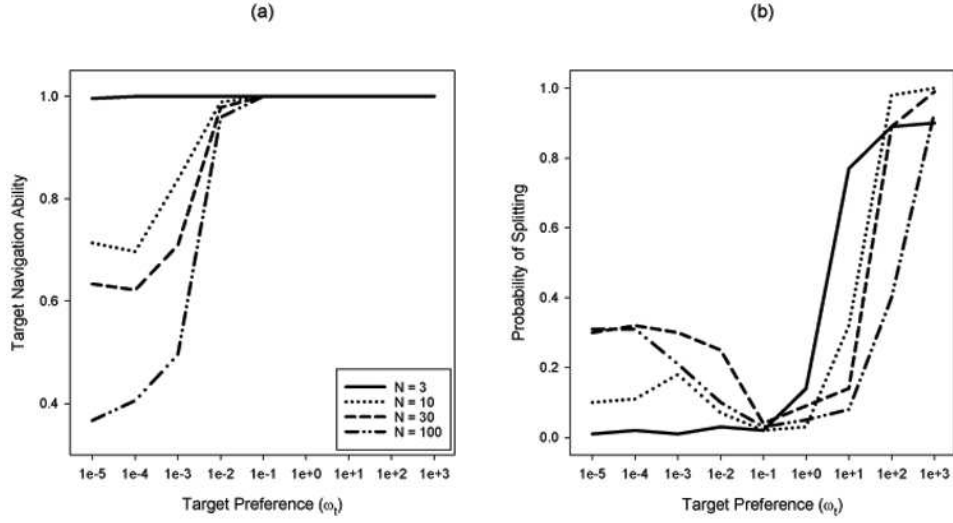


Figure 1: Parametrising target preference for coherent directed groups. For social groups ($w_s = 1$) of varying size (N) in an obstacle-free environment, we plot: (a) average proportion of distance travelled parallel with target trajectory; (b) probability of a group splitting; (recorded after 1000 time steps) as a function of baseline target preference (w_{t0}). We observe that beyond a critical value ($0 < w_t \leq 0.1$), dependent on N , navigation occurs directly along the target trajectory. This common direction appears to improve group cohesion reducing the probability of splitting but as w_{t0} increases further social preference is overwhelmed resulting in an increased proportion of groups splitting.

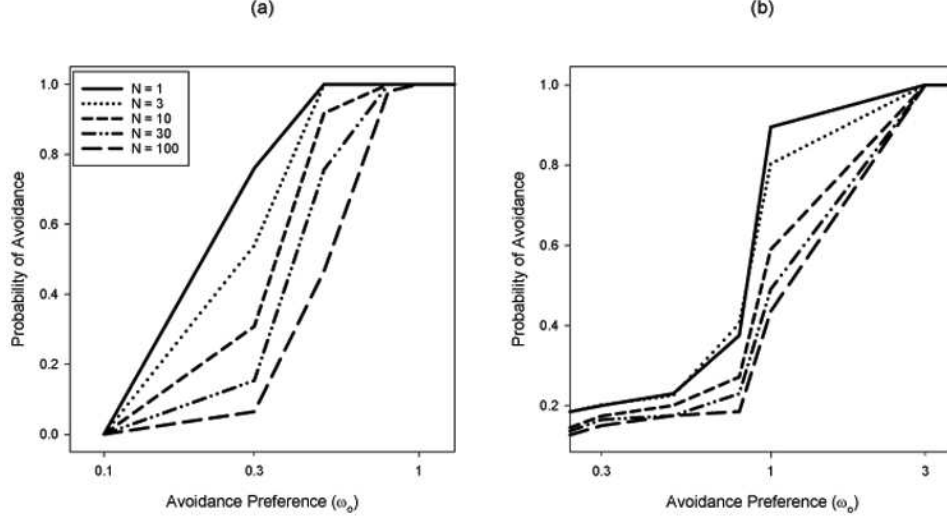


Figure 2: Avoidance of an obstacle does not guarantee avoidance of an array. For social groups ($w_s = 1$) of varying size (N) and baseline target preference ($w_{t0} = 0.1$) we plot the probability of avoiding the region bounding an array containing: (a) a single obstacle; (b) 25 obstacles uniformly arranged on a square grid at 500 metre intervals; (recorded after 1000 time steps) as a function of avoidance preference (w_o). For each, group target trajectory intersects the array at an angle which minimises the probability of avoiding all obstacle given no avoidance behaviour. As expected the probability of avoidance increases with w_o . However, this relationship is not linear but instead shows a sharp step at a critical value of preference particularly evident in (b). In common with previous studies [9] there appears a dependence upon N , with smaller groups displaying a higher propensity for avoidance. We note that the probability of avoiding all obstacles in case (b) (not shown) is qualitatively similar to (a) with transitions appearing at marginally lower values of preference. Consequently, groups demonstrate total avoidance of all obstacles in (b) prior to any avoidance of the array as a whole.

324 In particular, we exploit the potential of an asynchronous update scheme to
325 implement varying types of underlying social networks which may influence
326 group decisions.

327 Figure 3 shows that different network structures have distinct effects on
328 both the probability of avoiding an obstacle array and the resulting group
329 structure. We see that groups which navigate according to a homogeneous
330 network show the least ability to avoid obstacles, but demonstrate little
331 disruption to group structure (measured by the probability of the group
332 splitting). Comparing subsequent groups to this benchmark we notice that
333 any degree of heterogeneity within a network produces a higher probability
334 of avoidance, but that this can be at a cost to group cohesion. This is
335 most notably the case for leadership groups, which demonstrate the highest
336 probability of avoidance but also a high probability of splitting. For these
337 groups we see that avoidance is related to the number of leaders, with fewer
338 influential individuals providing the highest levels of avoidance. The number
339 of leaders does not affect splitting, which remains high. Clustered groups
340 appear to follow a pattern similar to that seen for group size. Here, as the
341 degree of clustering is increased, thus reducing the number of individuals
342 per cluster, we observe an increase in avoidance. This is matched by an
343 increase in the probability of splitting suggesting that clusters may begin to
344 act independently as their size is reduced.

345 For all networks the probability of avoidance shows a bimodal distribu-
346 tion in that, for a given simulation, either all group members traverse the ar-
347 ray, or all successfully avoid the array. This is of particular significance when
348 considered with figure 4 which maps the trajectories of groups responding to
349 the array. Despite varying probabilities of avoidance we see only marginal
350 differences between movement patterns. This suggests that avoidance is lim-
351 ited by the ability of a group to initiate an avoidance response rather than
352 an ability to perform the action. The horizontal trajectories seen for lead-
353 ership networks (panel (d)) are likely due to a loss of contact with the lead
354 individual during separation. A lower preference for other group members
355 increases the probability of separations becoming permanent resulting in this
356 self-navigation through the array.

357 Motivated by previous studies [6, 24], we then introduce groups which
358 contain individuals with heterogeneous abilities, in this case the preference
359 for avoidance and target navigation, i.e. $(w_o)_i = w_o + w_h * N(0, 1)$ and
360 similarly for the target weighting for each individual i . The results shown
361 in figure 5 demonstrate that as the magnitude of heterogeneity is increased
362 groups experience an increased disruption to group cohesion and reduced
363 probability of avoidance. This suggests that the relative variation of avoid-

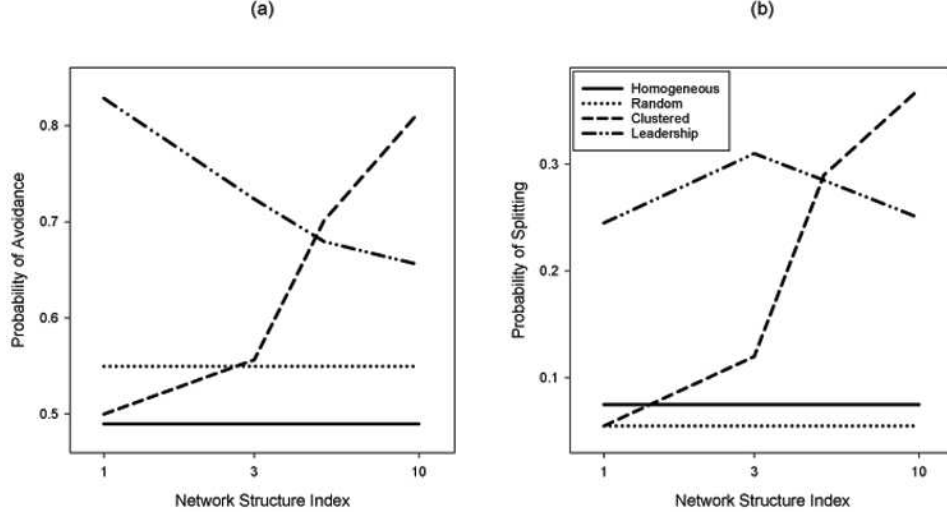


Figure 3: Heterogeneous social structure promotes obstacle avoidance.

For social groups ($w_s = 1$) of 30 individuals with baseline target preference ($w_{t0} = 0.1$) and avoidance preference ($w_o = 1$) intersecting an array containing 25 obstacles uniformly arranged on a square grid at 500 metre intervals, we plot: (a) probability of avoiding a region bounding the array; (b) probability of a the group splitting; (recorded after 1000 time steps) for various examples of underlying social network (homogeneous, random, clustered and leadership), as a function of network structure index indicating the precise number of clusters or leaders in respective network types (homogeneous and random networks are invariant). We observe that homogeneous groups display the least avoidance ability, generally followed by random networks. Clustered networks produce increasing avoidance and splitting with the number of clusters. Groups which employ a single leader exhibit the highest levels of avoidance but as the number of leaders increases avoidance is reduced.

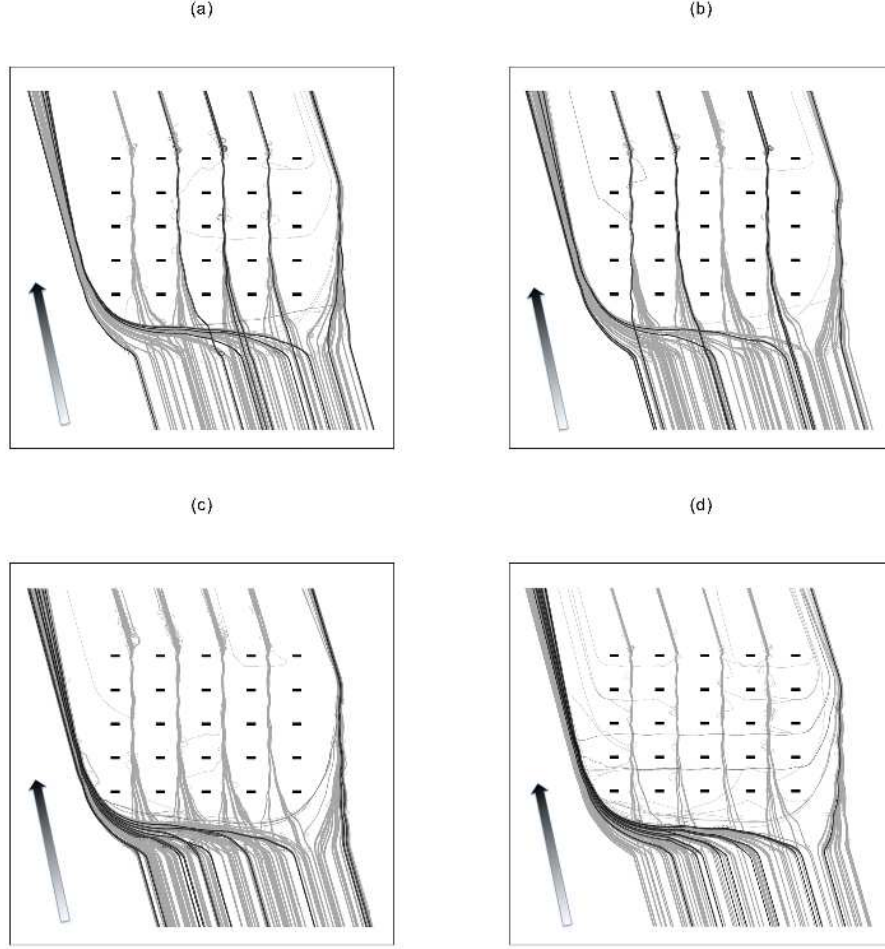


Figure 4: Similar movement patterns for distinct network structures. Mapped trajectories for groups with baseline target ($w_{t0} = 0.1$) and avoidance preference ($w_o = 1$) intersecting an array which contains 25 obstacles uniformly arranged on a square grid at 500 metre intervals and: (a) homogeneous; (b) random; (c) clustered; (d) leadership; underlying network structures. Each plot displays trajectories for 100 groups (light grey) of 30 individuals. 10 groups are highlighted (dark grey) with a focal individual (black). In (d) this focal individual represents the group leader. These plots can be compared to empirical data presented in [44]. We observe similar patterns of movement for all networks with only marginal differences in coherence ((b) shows less splitting) and cohesion ((c) shows high and (d) low density reflecting neighbour distances). See also supplementary movies S1a - S1d, corresponding to the panels in this figure.

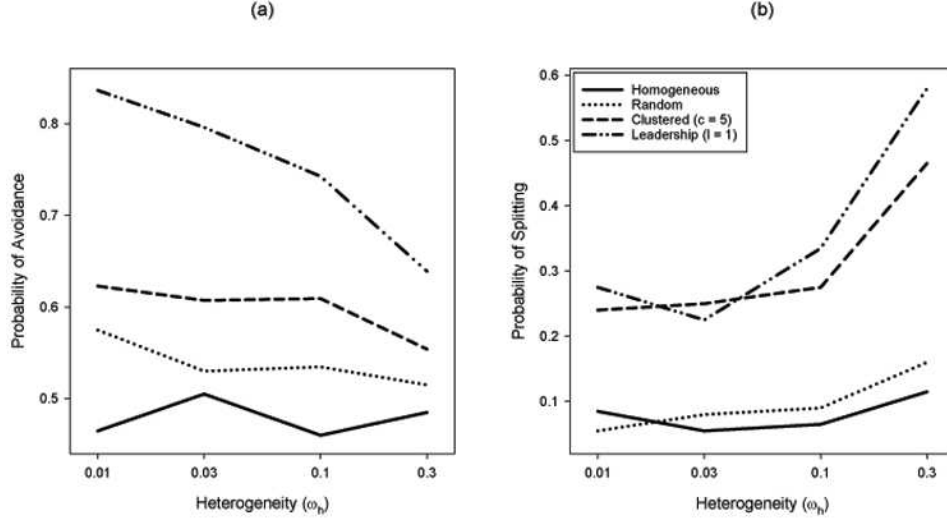


Figure 5: Variable ability reduces avoidance and group cohesion. For social groups ($w_s = 1$) of 30 individuals with baseline target preference ($w_{t0} = 0.1$) and avoidance preference ($w_o = 1$) intersecting an array containing 25 obstacles uniformly arranged on a square grid at 500 metre intervals, we plot: (a) probability of avoiding a region bounding the array; (b) probability of a the group splitting; (recorded after 1000 time steps) for various examples of underlying social network (homogeneous, random, 5 clusters and a single leader), as a function of heterogeneity w_h (magnitude of variation in avoidance and baseline target preferences). We observe that groups with a single leader are the most affected by changing heterogeneity showing a decrease in avoidance and increase in splitting as abilities become more variable. Clustered networks also induce this pattern although it is less pronounced. Groups with homogeneous and random networks appear largely unaffected by changes in heterogeneity showing only at small increases in splitting at high levels.

ance and target preferences alters the balance towards target navigation. In general, we see that groups which rely on fewer individuals for navigational decisions are more affected by this variation.

In order to assess whether the collisions observed by empirical studies could be explained by an increased risk as a result of environmental conditions, we vary the magnitude of movement error and the radius of attraction, the limit of an individuals sensory zone, to simulate turbulence and visibility respectively. Figure 6 shows that in both cases as parameters are varied to simulate poorer environmental conditions groups which rely on a particular individual for navigation are significantly influenced, transitioning from

374 showing the most avoidance to the least. In the case of turbulence this result
 375 contradicts [7], which shows asocial groups navigate more effectively in vari-
 376 able environments than their social counterparts. However, the trajectories
 377 mapped in panel (b)(i) (when compared with figure 4(a)) support the idea
 378 that at least for social groups, target navigation is significantly affected by
 379 turbulence. In highly turbulent environments groups are less likely to fol-
 380 low the target trajectory intersecting the array, and so appear to improve
 381 their ability to avoid obstacles. For those groups which are able to maintain
 382 accurate target navigation, such as those which rely on a particular individ-
 383 ual, we have clear evidence that avoidance behaviour is susceptible to poor
 384 conditions. Our simulations suggest that in all groups environmental condi-
 385 tions affect avoidance behaviour, but the response is dependent on the social
 386 structure. The increased dependence on local decisions makes it less likely
 387 that the groups will enter the array but the effect of this is to cause greater
 388 disruption to the group which may have significant effects on other fitness
 389 costs not captured here.

390 Despite the erratic movements of groups in turbulent environments (panel
 391 (b)(i)), individuals retain the ability to avoid obstacles and we observe no
 392 collision risk for any level of turbulence. This is not the case in environments
 393 which simulate low visibility. We find that, as visibility is reduced, group
 394 show much later and more extreme avoidance responses resulting in the
 395 stepped movement patterns in panel (b)(ii). Here, we see that for some
 396 groups the loss of pre-emptive avoidance means they are no longer able to
 397 react in time to prevent intersections with obstacles.

398 Finally, we investigate the effect of introducing a variable target prefer-
 399 ence simulating the desire of groups to follow a direct migratory route with
 400 high fidelity. This is implemented by an allowing an increase in selection
 401 of an individual when the local angular deviation from the route increases.
 402 For comparison we parametrise the component of variable target preference
 403 such that with an inflated avoidance preference of $w_o = 3$ the avoidance rate
 404 for a group of 30 individuals is equivalent to the typical case. It should be
 405 noted that the use of a variable target preference with this parametrisation
 406 does not alter the results seen for groups in obstacle-free or single obstacle
 407 environments. The plot in figure 7(a) shows that this need for route fidelity
 408 significantly alters the relationship between avoidance and group size, re-
 409 versing the trend from non-linearly decreasing with group size to show a
 410 marginal increase. The change in avoidance is most noticeable for smaller
 411 groups which show a reduction in avoidance whereas the values for larger
 412 groups remain relatively unchanged. In comparison with groups which apply
 413 no cost to avoidance, the mapped trajectories shown in panel (b) show that,

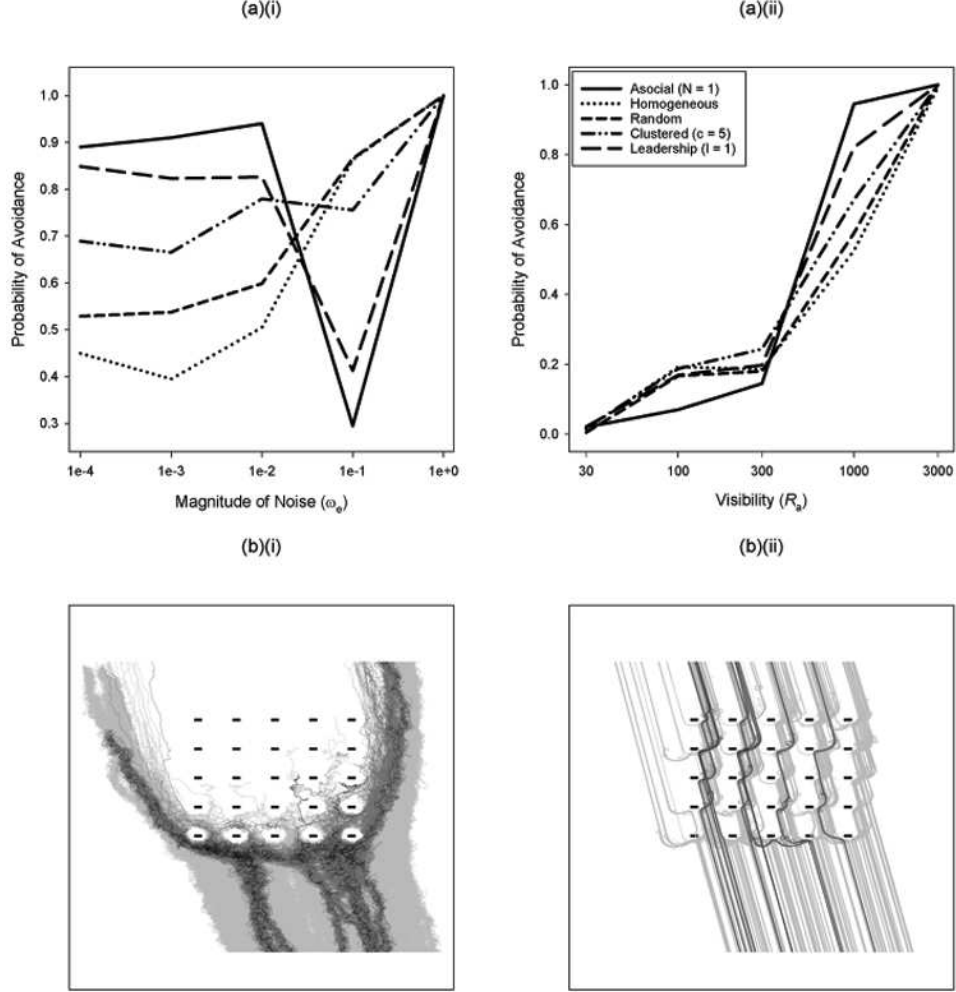


Figure 6: Leaderless groups appear less susceptible to environmental factors. For social groups ($w_s = 1$) with baseline target preference ($w_{t0} = 0.1$) and avoidance preference ($w_o = 1$) intersecting an array containing 25 obstacles uniformly arranged on a square grid at 500 metre intervals, we plot: (a) probability of avoiding a region bounding the array (recorded after 1000 time steps) as a function of: (i) turbulence (w_e); (ii) visibility (R_a); for various social structures; (b) trajectories for 100 groups of 30 individuals (light grey) with underlying homogeneous network in an environment where: (i) $w_e = 0.1$ (increased from 0); (ii) $R_a = 100$ (decreased from 1000). 10 groups are highlighted (dark grey) with a focal individual (black). Groups with a leader initially display the most avoidance but as conditions worsen they transition to showing the least. Mapped trajectories show that when visibility is reduced collisions can occur.

414 despite evidence indicating an earlier initiation of avoidance, the response is
415 limited by the increased route fidelity. Consequently, groups are much less
416 likely to avoid the array when required to travel across the corridors between
417 columns of obstacles.

418 Discussion

419 We have outlined a method by which obstacle interactions can be incorpo-
420 rated into an asynchronous individual-based model without compromising
421 biological realism. The novel mechanism by which our model balances social
422 and navigational forces creates a trade-off between group interactions and
423 responses to environmental cues. Social interactions are dependent not only
424 on social preference but also relative distance, meaning that groups with
425 decreased nearest neighbour distance will exhibit more social tendencies.
426 When individuals interact socially they pass on indirect information about
427 environmental cues. This information is necessarily ‘noisy’, but averaging
428 across multiple neighbours can filter noise [7]. A complementary study [48]
429 shows that the noise experienced by individuals can have an important role
430 on group dynamics in the presence of obstacles – where this noise is small,
431 the group may be too inflexible to adjust to the presence of obstacles and
432 maintain cohesion.

433 For environmental cues, such as target navigation, where the directional
434 information is similar for all group members, averaging provides a robust
435 method by which individuals can combine knowledge to formulate a cohe-
436 sive group response. However, when individuals are subject to conflicting
437 information averaging can result in an inappropriate group decision, as can
438 be case for obstacle avoidance where response is highly dependent upon
439 spatial position. This is of particular relevance where the ideal avoidance
440 strategy is unclear, for example when an obstacle is spaced equally either
441 side of the group centre. In such situations the movements of an informed
442 individual or cluster can sufficiently influence group decisions to initiate a
443 successful avoidance response [6] and break the decision deadlock [49]. This
444 is consistent with our results for varied group sizes which show an increase
445 in avoidance for groups comprising fewer individuals. Here, average informa-
446 tion is obtained across a smaller sample thus allowing for a greater bias from
447 particular individuals, with leaders emerging more frequently. When infor-
448 mation cannot be resolved to achieve a unified group decision this results
449 in the formation of localised subgroups which overwhelm the social bonds
450 holding the group together and separate away in a different direction.

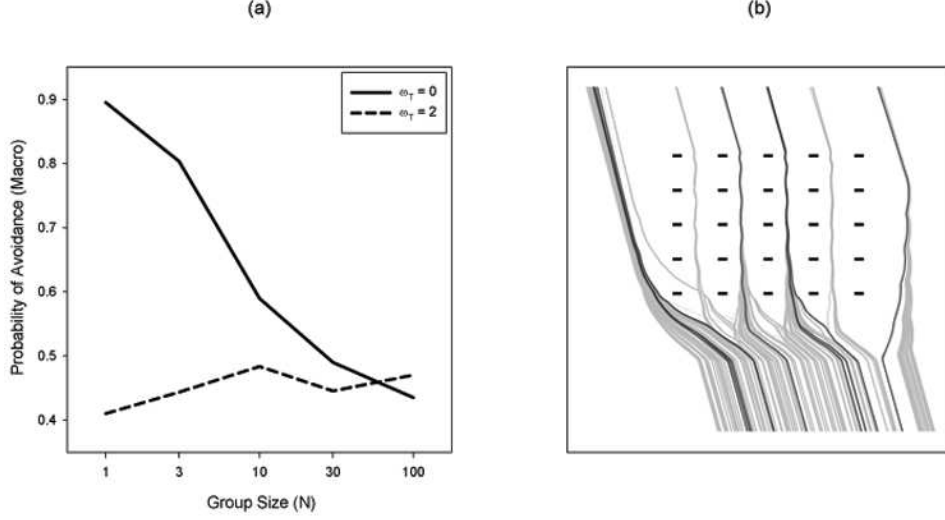


Figure 7: Route fidelity outweighs collision risk for small groups. For social groups ($w_s = 1$) with baseline target preference ($w_{t0} = 0.1$) intersecting an array containing 25 obstacles uniformly arranged on a sEnergetic benefitquare grid at 500 metre intervals, we plot: (a) probability of avoiding a region bounding the array (recorded after 1000 time steps) for different sets of avoidance and variable target preference ($w_o = 1, w_{t1} = 0$ and $w_o = 3, w_{t1} = 2$), as a function of group size (N); (b) trajectories for 100 groups of 30 individuals (light grey) with avoidance ($w_o = 3$) and variable target preference ($w_{t1} = 2$). Groups with no consideration for route fidelity show a non-linear relationship where avoidance decreases with group size. When an cost to avoidance, due to a lack of fidelity, is introduced the relationship with group size is reversed. Mapped trajectories show few avoidance manoeuvres which cross multiple corridors between columns. Groups are most likely to traverse the array along the nearest corridor in the target direction. Exceptions occur when this is an outer corridor with groups instead choosing to navigate outside the array.

451 Our results show that underlying social networks produce significant dif-
 452 ferences to both group structure and navigational response. When compared
 453 with the leaderless homogeneous case described above, we find that for any
 454 underlying networks where preference is shown towards interactions with
 455 particular individuals, groups demonstrate a higher probability of avoidance.
 456 This is consistent with the similar improvements shown elsewhere [50]. This
 457 behaviour results from an increased bias within the group decision making
 458 process. Consistent with existing studies we observe that groups with fewer
 459 influential individuals provide the most effective response to contradictory
 460 environmental information [24]. In contrast with this type of leadership, ex-
 461 amples which simulate clustering show the emergence of smaller independent
 462 groups showing less cohesion but maintaining an ability to initiate avoidance
 463 actions without clearly defined leaders.

464 Whilst a reliance upon fewer individuals for navigation can be beneficial
 465 it is also less robust to sensory variability [7]. When variation is applied to
 466 both target and avoidance preferences the ability of such individuals to lead
 467 a group may not justify the influence which neighbours show towards them
 468 resulting in impaired navigational responses. Conversely, we find that when
 469 movement error is applied to simulate turbulence groups which navigate
 470 either asocially or with a single leader maintain coherent target navigation
 471 even in highly disruptive environments. Unlike in Codling et al. [7] where
 472 this result represents a positive outcome, in our model avoidance ability is
 473 not maintained at a relative level and whilst other groups avoid the array
 474 as a result of inaccurate navigation those which maintain target navigation
 475 consequently intersect the array more frequently. However, it is clear that
 476 even at high turbulence individuals maintain a safe distance from obstacles
 477 which suggests in our chosen parameter range that the risk of collision is
 478 effectively zero. This is not the case when the sensory range of individuals
 479 is reduced, mimicking conditions of poor visibility [7]. Collisions are observed
 480 when the sensory range falls below the radius of obstacle repulsion thus
 481 reducing the distance in which individuals have to respond to initiate an
 482 avoidance manoeuvre.

483 Throughout this study we have assumed that collision rates are the result
 484 of deficiencies in sensory ability. We challenge this assumption by suggesting
 485 that all groups may in fact possess an ability to avoid obstacles but instead
 486 choose to enter arrays because of strong route fidelity related to migratory
 487 efficiency. By introducing a variable element to target preference which pro-
 488 duces an increasing desire to select target navigation as individuals deviate
 489 further away from the optimal target trajectory, we show that groups con-
 490 taining fewer individuals are much more likely to voluntarily enter the array.

491 This has potentially important consequences for groups that are weakened,
492 for example by lack of food, and may make different times of the year more
493 important for collision vulnerability.

494 The ultimate goal of this modelling study is to quantify the risk of avian
495 collisions with wind turbines. We recognise that at present the model out-
496 lined here is limited to specific scenarios in which individuals show no verti-
497 cal avoidance. In reality, large-scale studies suggest that in good conditions
498 birds, such as geese, favour vertical avoidance. Our modelling methods are
499 amenable to generalisation to three-dimensions [31] where data are available.
500 However, through simulations with an array containing multiple obstacles
501 we demonstrate that the cumulative avoidance response to those obstacles
502 is sufficient to produce movement patterns which can be compared to those
503 recorded by empirical studies. We show that by selecting reasonable param-
504 eter values we can reproduce estimated avoidance rates. Furthermore, we
505 use the model to explore conditions which are difficult to assess empirically.
506 These results reinforce the suggestion that birds are most at risk of collision
507 when conditions reduce detection distance, for example during nocturnal
508 navigation.

509 The effect of social networks has not previously been modelled in the
510 context of obstacle avoidance. We have shown in this study that social in-
511 teractions can affect the ability of a group to perform suitable avoidance
512 responses and it would therefore be ecologically informative to include real-
513 istic social networks when assessing risk. The structure of networks has been
514 shown to have considerable impact on group behaviour, in ecological exam-
515 ples [6, 36] as well as in other biological settings [51]. Compared with our
516 simple examples, goose social networks have been shown to be more complex
517 and highly variable [21, 22]. The relationship between in-flight communica-
518 tion networks and important social structures, such as foraging groups or
519 family grouping, has been shown to have complex correlations which make it
520 difficult to interpolate between them [23]. Therefore, caution must be exer-
521 cised in making social inferences from in-flight interactions and consequences.
522 Our results indicate that movement patterns, similar to those obtained by
523 current radar studies which assess collision risk, cannot be used to infer the
524 structure of social networks. This observation highlights the need for greater
525 focus on the motion of individuals in the context of obstacle avoidance. To
526 address these deficiencies new experimental approaches are necessary so that
527 individual-based social network models can be verified and utilised to their
528 full potential to predict avoidance rates *in silico*. With these advances it
529 may be possible to inform decisions regarding the impact on birds prior to
530 the construction of wind farms.

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